Title: Adjustment of Forest Ecosystem Root Respiration as Temperature Warms

Running Title: Root Respiration and Climatic Warming

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Abstract

Adjustment of ecosystem root respiration to warmer climatic conditions can alter the autotrophic portion of soil respiration and influence the amount of carbon available for biomass production. We examined 44 published values of annual forest root respiration and found an increase in ecosystem root respiration with increasing mean annual temperature (MAT), but the rate of this cross-ecosystem increase (Q_{10} = 1.6) is less than published values for short-term responses of root respiration to temperature within ecosystems (Q_{10} = 2 to 3). When specific root respiration rates and root biomass values were examined, there was a clear trend for decreasing root metabolic capacity (respiration rate at a standard temperature) with increasing MAT. There also were tradeoffs between root metabolic capacity and root system biomass, such that there were no instances of high growing season respiration rates and high root biomass occurring together. We also examined specific root respiration rates at three soil warming experiments at Harvard Forest, USA, and found decreases in metabolic capacity for roots from the heated plots. This decline could be due to either physiological acclimation or to the effects of co-occurring drier soils on the measurement date. Regardless of the cause, these findings clearly suggest that modeling efforts that allow root respiration to increase exponentially with temperature, with Q_{10} values of 2 or more, may over-predict root contributions to ecosystem CO_2 efflux for future climates and underestimate the amount of C available for other uses, including NPP.

Key Words: root respiration, acclimation, root biomass, climatic warming, soil warming

Increases in terrestrial ecosystem respiration as temperatures warm could create a positive feedback that causes atmospheric CO_2 concentration, and subsequently global temperature, to increase more rapidly (Woodwell and Mackenzie 1995; Cox et al. 2000). If plant tissue respiration acclimates to temperature over time, this feedback loop will be weakened (Luo et al. 2001; King et al. 2006), reducing the potential temperature increase. However, time-dependent acclimation of plant respiration to warmer temperatures is not included in most coupled climate-carbon models (King et al. 2006). For foliage, ecosystem modeling studies show that including temperature acclimation can have a substantial effect on estimates of C exchange and net primary productivity (NPP) (Wythers et al. 2005). For example, Hanson et al. (2005) modeled effects of CO_2, temperature, precipitation and ozone on carbon and water cycles for an upland oak forest. When acclimation of leaf respiration to warming was included in the model, the combined influence of the multiple factors on net ecosystem exchange (NEE) for the year 2100 became a 20% increase rather than a decrease.

Like leaves, fine roots are physiologically very active. On an annual basis, root-associated respiration in forested ecosystems contributes about one half of annual soil respiration (Hanson et al. 2000; Högberg and Read 2006), but the potential for ecosystem root respiration to acclimate to warmer climates is not considered by most modeling efforts predicting future forest C cycles. Instead, root respiration is typically allowed to increase exponentially with warmer temperature (White et al. 1999). In this report, we first use published values of annual root respiration to assess the cross-ecosystem rate of increase with temperature. Then we examine the potential for trade-offs between root metabolic capacity and biomass in regulating ecosystem root respiration, using published values for mid-growing season root specific respiration rates and root biomass. Finally, we determine if relationships that occur across ecosystems adapted to different climates might also exist within an ecosystem that is subjected to warming, by examining results from soil warming studies, including recent measurements of fine root respiration made at three warming experiments at Harvard Forest, USA.

Results

Annual root respiration increased exponentially with mean annual temperature (MAT) across forest ecosystems (Fig 1). The change in respiration with MAT is equivalent to a Q_{10} of 1.63 when all data are considered ($r^2 = 0.45$, $P < 0.001$) and 1.56 when only temperate and boreal data

are considered ($r^2 = 0.33$, $P < 0.001$). Mid-growing season specific respiration rates also tended to increase with MAT (Fig 2A), but this apparent effect occurs because the measurements were made at warmer temperatures for samples from locations with higher MAT. When specific respiration rates are adjusted to a common temperature of 16 ^{o}C, as an indicator of metabolic capacity, there is a clear decline in respiratory capacity as MAT increases (Fig 2B). Across ecosystems, root biomass was not correlated with MAT. Instead, root biomass was negatively correlated with mid-growing season fine root respiration rate, especially for temperate forests (Fig. 3A). Some of the differences in respiration rates among sites are due to different measurement temperatures, which tend to cause lower mid-growing season specific root respiration rates to occur for cooler, boreal forest samples. When respiration rates are adjusted to a common temperature (Fig. 3B), the trade-off between respiration rate and root biomass still exists, with boreal and non-boreal forests appearing to follow a common relationship. No cases of high respiration rate and high fine root biomass occurring together were found (Fig 3).

We noted no obvious differences among methodologies for responses to temperature of annual root respiration (Table 1) or specific root respiration (Table 2). However, low sample sizes for some methods and variation in the actual techniques applied within each methodological category compromise our ability to draw any clear conclusions regarding potential methodological biases.

Respiration rates at field soil temperature for heated plots from the Harvard Forest soil warming studies were 45% greater on average than for unheated plots (Fig. 4A). This significant increase ($P = 0.009$) occurred , with no experiment by warming treatment interaction ($P = 0.133$). This enhancement is lower than the 52 to 93% increase that would be predicted by typical Q_{10}'s for forest root respiration of 2.0 to 3.0 (Table 2). As a result, respiration rates at the constant reference temperature of 18 ^{o}C were significantly lower ($P = 0.003$) for the heated plots, by an average of 23% (Fig. 4B), with no experiment by warming treatment interactions ($P = 0.139$).

The differences between respiration rates at ambient temperature and the 18 ^{o}C reference temperature were used to calculate Q_{10} values for short-term temperature increases for the control and heated plots. These averaged 3.0 ± 0.1 (mean ± 1 s.e.) across the three experiments, with no differences in short-term Q_{10} occurring among warming treatments or experiments. We also used respiration rates at ambient temperature for control and heated plots (i.e. treatment means

from Fig. 4A) to estimate a long-term Q_{10} for each of the three experiments. These were all far lower than the short-term Q_{10} of 3.0, with values ranging from 2.3 for the 1991 experiment, to 1.9 for the 2003 experiment, to 0.91 for the 2006 experiment.

Root N concentration did not differ among treatments or experiments for the Harvard Forest studies (Fig. 4C). Therefore, respiration rate per unit N at the 18 ^{o}C reference temperature was significantly lower for roots from heated plots (Fig. 5). Soil moisture contents were 11 to 18% lower for the heated plots (Table 3), with the treatment effect being significant for two of the three experiments.

Discussion.

Cross-Ecosystem Relationships between Root Respiration and MAT.

Reported values of Q_{10} for root respiration are often between 2 and 3 (Table 2 and references therein). The median and mean Q_{10} values for the studies reported in Table 2 are 2.4 and 2.7, respectively. These are for short-term increases in temperature associated with seasonal variations in soil temperature or derived from measurements of root respiration across a range of temperatures during one sampling period. Comparisons across ecosystems, however, show a much lower rate of increase in annual root respiration as MAT increases (Q_{10} = 1.6, Fig. 1).

Across ecosystems, proportional increases in gross primary productivity (GPP) and autotrophic respiration with MAT have been reported (Litton et al. 2007), such that as GPP increases, the absolute C flow to all sinks also increases (biomass and respiration, above- and belowground). Aboveground net primary productivity (ANPP) in forest ecosystems tends to increase with MAT. For example, the data of Vogt et al. (1996), for 101 forested study sites, can be used to estimate a rate of increase in ANPP with MAT that is equivalent to a Q_{10} of 1.7 (r^2 = 0.24, $P < 0.001$). Excessively high rates of ecosystem root respiration would not allow for high aboveground productivity (Vogt et al. 1996), but the more tempered increase in ecosystem root respiration with MAT, illustrated in Figure 1, avoids excessive ecosystem root respiration for warm climates, allowing increases in productivity to occur. Similar rates of increase with MAT for forest ecosystem root respiration (this study) and ANPP (Vogt et al. 1996) are consistent with the idea that total autotrophic respiration utilizes a constant proportion of GPP (Litton et al. 2007). It should be noted, however, that others have not always found such relationships. For

example, Bond-Lamberty et al. (2004) did not find a relationship between soil autotrophic respiration and aboveground, belowground or total NPP for 17 forested sites.

Across forest ecosystems, annual ecosystem root respiration increases at a much lower rate than occurs within ecosystems in response to short-term temperature changes. This suggests that ecosystems from warmer climates must have either lower root biomass or roots with lower metabolic capacity (i.e. lower respiration rate at a given temperature). Our examination of published fine-root specific respiration rates and biomass suggests both mechanisms likely play a role. The increase in mid-growing season fine-root specific respiration rate with increasing MAT (Fig 2A) is representative of a Q_{10} of about 1.2, far less than the typical Q_{10} for fine root respiration associated with short-term changes in measurement temperature (mean 2.7, range 1.9 to 5.6, Table 2). Using specific respiration rates adjusted to a common temperature of 16 ^{o}C as an indicator of metabolic capacity, there is a tendency for declining metabolic capacity with increasing MAT (Fig. 2B). This would suggest that root system respiratory capacity is acclimated to growth temperature. Essentially, fine roots are constructed with a smaller metabolic machine that runs faster due to warmer conditions, allowing root functions to be performed without unneeded C loss. Under such a scenario, the maximum respiratory rate might actually be similar for plants from warm and cold locations, with the temperature at which the maximum rate occurs being lower for the cold location.

One mechanism that can result in lower metabolic capacity is the construction of plant tissues with lower protein and amino acid contents. Such roots would have lower N concentrations and lower respiration rates, in agreement with the many reports of strong correlations between tissue N and respiration rate (Ryan et al. 1996; Zogg et al. 1996; Burton et al. 1996, 2002; Atkinson et al. 2007). Tjoelker et al. (1999) found conifer seedlings grown at warmer temperatures had much lower foliar N concentrations associated with lower dark respiration rates at a given temperature, and Atkinson et al. (2007) found temperature acclimation in roots of herbaceous plants grown at warmer temperatures that was partially, but not totally, explained by lower tissue N. For the experiments described in Table 2, there is indeed a strong relationship between tissue N concentration and specific respiration rate at the 16 ^{o}C reference temperature (Fig. 6). The two instances of warm MAT for which root N data were available both had low root N and low specific respiration rates (Table 2). It should be noted that low root N and specific respiration rates were also common in many boreal forests (Table 2), presumably due to nutrient limitation

in cold, wet, low productivity forests with low rates of nutrient release, rather than acclimation to warm temperatures.

There is considerable noise around the linear trends for the relationships between specific respiration rates and MAT (Fig. 2). This is likely due to in part to site-to-site variation in nutrient and moisture availability and their effects on GPP, net growth and autotrophic respiration. However, the ability for ecosystem root activity to be constrained by reductions in root biomass, rather than reductions in metabolic capacity, also appears to play a role. In some cases, fairly high root respiration rates occurred at warm locations (Fig. 3), but in these situations, root biomass was consistently low. There were no instances of high mid-season respiration rates and high root biomass occurring together.

Root Respiration in Soil Warming Experiments.

Our comparisons across ecosystems and climatic zones indicate that stand-level root respiration in forests is constrained under warm conditions by either low root biomass or low respiratory capacity. Of more concern with regard to climatic change is whether or not root biomass or respiratory capacity will change *within* an ecosystem as climate warms. Previous soil warming experiments in forests have examined soil respiration, but generally do not provide information on either specific root respiration rates or root biomass. Still, changes in soil respiration over time provide some insight regarding possible changes in root system respiration.

Ecosystem warming experiments typically show significant increases in soil respiration in the first one to three years of warming, but the enhancement tends to lessen over time (Peterjohn et al. 1994; Rustad et al. 2001; Melillo et al. 2002, 2004; Eliasson et al. 2005; Bronson et al. 2008). This transient response is often attributed to rapid decomposition of labile soil C compounds in the first years of soil warming (Peterjohn et al. 1994; Melillo et al. 2002, 2004; Eliasson et al. 2005; Davidson and Janssens 2006). After this period, available substrate could become more limiting and the heterotrophic portion of soil respiration would not be greatly elevated. Still, soil respiration should remain measurably elevated due to greater autotrophic root respiration, unless root biomass or respiratory capacity has changed. If root biomass and metabolic capacity are unchanged, then soil temperature increases of 4 to 5 ^{o}C would increase root respiration from 32 to 73%, assuming typical Q_{10}'s for root respiration of 2 to 3. Root respiration tends to produce about one half of annual soil CO_2 efflux for forested ecosystems (Hanson et al. 2000; see also

Table 1 and references therein). Thus if root biomass and root metabolic capacity are unchanged by soil warming, the 4 to 5 ^{o}C warming typical of forest soil warming experiments should result in an increase of 16 to 37% in soil respiration due to increased ecosystem root respiration alone. Instead, soil respiration rates were reported to be 11% greater after two years of 5 ^{o}C soil warming in black spruce (Bronson et al. 2008) and only 5% greater after seven years of 5 ^{o}C soil warming in a mixed hardwood forest (Melillo et al. 2002). Even very low contributions of root respiration to soil respiration (circa. 20%, Melillo et al. 2002), should cause increases in soil respiration of 8 to 15% for a 5 ^{o}C warming and Q_{10} between 2 and 3.

In the long-term, heterotrophic respiration in these experiments should be approaching equilibrium with detrital inputs after enhanced loss of labile soil C has subsided. If detrital inputs in these experiments were little changed by warming, or somewhat greater due to enhanced productivity (Rustad et al. 2001; Strömgren and Linder 2002), then soil respiration would have to be measurably increased if root-associated respiration increased exponentially with temperature in accordance with published Q_{10} values. Since this has not happened, increases in root system respiration in soil warming experiments would appear to have been constrained by either changes in root biomass or changes in root metabolic capacity. Bronson et al. (2008) found that heating soil alone, or soil and air, resulted in reduced root biomass for 12 year old black spruce plantations, in agreement with this assumption.

Our examination of fine root specific respiration rates for three soil warming experiments at Harvard Forest suggests decreases in metabolic capacity are occurring, to some degree, in those experiments. By comparing heated and control plots from the three experiments, we have documented long-term values of Q_{10} for root respiration that are much lower than short-term Q_{10} values for the same locations. These findings are in agreement with previous examinations of whole-plant respiration in agricultural and floricultural warming experiments, where long-term Q_{10} values, based on comparisons across growth temperatures, often were between 1.2 and 1.6, and sometimes were less than 1.0 (Frantz et al. 2004; van Iersel 2006). Lower long-term Q_{10} and lower respiration rates at the constant reference temperature for roots from warmed soils of all three experiments at Harvard Forest may indicate physiological acclimation to warmer temperatures (Atkin et al. 2000), but they also may simply be a consequence of drier soils on the heated plots (Table 3), as dry soils have previously been shown to reduce root respiration (Burton et al. 1998; Bryla et al. 1997, 2001; Moyano et al. 2008).

True acclimation could occur is through the construction of fine roots with lower root amino acid and protein concentrations, as discussed in the preceding section. We did not see evidence for this, but instead found lower respiration rates per unit N in fine roots from warmed soils. Thus either drier soil conditions are responsible, or temperature acclimation associated with substrate availability and/or sink strength, rather than enzyme availability, has occurred. Tjoelker et al. (2008) compared jack pine foliar respiration measured at 20 ^{o}C in three North American common gardens and found seasonal acclimation in dark respiration, with rates inversely tracking seasonal changes in temperature. Temperature acclimation was associated with variations in N and soluble carbohydrates, indicating that regulation by both enzyme and substrate availability was involved. Lee et al. (2005b) found similar mechanisms underlying foliar temperature acclimation in oak and maple seedlings. These results are consistent with the hypothesis that over sufficiently long periods (weeks to a year), autotrophic respiration is linked to photosynthesis (Saxe et al. 2001). Alternatively, Atkin and Tjoelker (2003) describe a mechanism by which acclimation can occur through adenylate control caused by demand for the products of respiratory activity being significantly less than the ability of the respiratory pathways to provide them (i.e. low use of ATP resulting in reduced regeneration of ADP). Acclimation associated with either substrate or adenylate control could occur without changes in tissue N concentration.

We have used respiration at a constant, intermediate temperature to assess acclimation, but it should be noted that additional methods for assessing acclimation, both within and across ecosystems, include determining the temperature of maximum respiration rate and assessing respiration at both cold and warm constant temperatures. The combination of these methods might help one determine whether the entire response curve for respiration vs temperature shifts right for plants grown at higher temperatures, or if the shape of the curve is altered. For the Harvard Forest warming plots, root respiration measurements made throughout a growing season might help elucidate the relative importance of dry soils and physiological acclimation in reducing root metabolic capacity, assuming such a sampling regime includes periods when precipitation inputs had been sufficient to eliminate soil moisture differences between treatments. Still, our one-time sampling at Harvard Forest makes it clear that specific root respiration rates did not simply increase exponentially with long-term warming in accordance with observed Q_{10} relationships for short-term temperature changes.

Effects of Co-occurring Changes Induced by Warmer Temperatures

Climatic warming can result in increased frequency of soil moisture deficits if precipitation inputs do not simultaneously increase enough in quantity and frequency to offset increased evaporative demand. In soil warming experiments, the co-occurring decline in soil moisture availability (Rustad et al. 2001) often influences ecosystem responses as much or more than temperature change (Saleska et al. 1999; Loik et al. 2000; Shaw and Harte 2001). As described above, drier soil conditions can result in reduced root respiration rates. The impact of periodic moisture deficits on annual ecosystem root respiration will depend on the duration and intensity of moisture deficits during the growing season. Reduced root respiration due to drought will decrease the annual C cost of root activity, but severe moisture deficits might also limit ecosystem photosynthesis and net productivity. Controlled studies that manipulate temperature and moisture, at a scale encompassing entire forest root systems, are lacking for forests, and the lack of multiple-factor, multiple-year experiments of ecosystem responses to global change factors limits our ability to make predictions of real-world future responses (Morgan 2002).

If moisture is sufficient, a warmer climate can increase rates of organic matter production and decomposition. In soil warming experiments, increased N mineralization has often occurred (Rustad et al. 2001; Strömgren and Linder 2002). Evidence to date from the Harvard Forest warming experiments suggests that the effects of warming on soil moisture status are not overriding the effects of higher temperatures, as N availability has increased (Melillo et al. 2002). Increased N availability has the potential to alter proportional allocation of C to above- and belowground sinks. Forests often respond to fertilizer N additions by decreasing root biomass (Haynes and Gower 1995, Ryan et al. 1996, Litton et al. 2007). Thus warming-induced enhancement of N availability provides a potential mechanism, reduced root biomass, which could result to the occurrence of little change or even reductions in ecosystem root respiration with warming, rather than exponential increases.

This paper has focused on responses of root system respiration to climatic warming, but similar responses are also possible for the fungal portion of the belowground absorbing network and for rhizosphere microbes dependent on substrates produced by live roots (exudates and sloughing). Both of these can contribute important portions of root-associated respiration. Allocation to mycorrhizal fungi has been reported to utilize from 0 to 22% of GPP in forest

ecosystems, with mycorrhizal mycelium contributing from 3 to 25% of soil respiration (Heinemeyer et al. 2007; Moyano et al. 2008). The response of mycorrhizal fungal respiration to temperature is not well understood, but recently both Heinemeyer et al. (2007) and Moyano et al. (2008) have reported that respiration of mycorrhizal hyphae did not respond to changes in soil temperature. Heinemeyer et al. (2007) did find significant decreases in ectomycorrhizal hyphal respiration as soils dried.

The alteration of N availability by warming could potentially have important effects on rhizomicrobial activity. Decreases in mycorrhizal abundance and activity (Wallenda and Kottke 1998; Treseder 2004; van Diepen et al. 2007) as well as community structure (Lilleskov et al. 2002) can occur in response to enhanced N availability in forest ecosystems, although occasional instances of little change and increases have also been noted (Treseder et al. 2007). Rhizosphere microbes can also be affected. Phillips and Fahey (2007) found N additions reduced microbial respiration and mycorrhizal colonization in a northern red oak plantation; reduced root biomass, microbial respiration and mycorrhizal colonization in a sugar maple plantation; and reduced only microbial respiration in a yellow birch forest. In all cases, N availability effects on microbial respiration were greater in the rhizosphere than bulk soil.

Despite the need for much more information regarding the responses of mycorrhizal fungi and rhizosphere microbes to altered environmental conditions, the evidence available suggests that exponential increases with climatic warming in their contributions to root-associated respiration are unlikely, due in part to the negative effects of co-occurring changes in moisture and nutrient availability.

Across ecosystems, root associated respiration tended to increase from cooler to warmer climates. However, the rate of increase across ecosystems was less than would be caused by exponential increases similar to those occurring for specific root respiration in response to short-term warming. In warmer climates, ecosystem root respiration was constrained by either lower root biomass or the production of fine roots with lower metabolic capacity. Our cross-ecosystem comparison found no occurrences of ecosystems with both large root biomass and high respiratory capacity in warm climates. It is not known if reductions in root biomass or specific respiratory capacity will occur within a given ecosystem in response to long-term climatic warming, but limited evidence from existing forest soil warming experiment suggests that decreases in both can occur in response to the combination warmer soil, drier conditions and

altered N availability predicted for warmer climates. Modeling efforts that allow root respiration to increase exponentially with temperature may be suitable for estimating effects of short-term climatic variation, but are likely to over-predict ecosystem root respiration rates following long-term climatic warming, and thus may underestimate the amount of C available for other uses, including NPP. To address this issue, there is a need for studies that manipulate temperature and moisture at scales that would encompass entire forest root systems. Data from such studies on the tissue and ecosystem level responses of roots, mycorrhizae and rhizosphere microbes, gathered across growing seasons and years, will allow modelers to better predict belowground C allocation for future climates, C available for aboveground productivity, and contributions of root systems to soil CO_2 efflux.

Materials and Methods

Effects of Temperature on Annual Ecosystem Root Respiration

Published values for annual forest root respiration from 44 stands were examined to assess the cross-ecosystem relationship between annual C efflux from root respiration and mean annual temperature (MAT) (Table 1). The MAT for the studies ranged -4.7 to 25.8 ^{o}C. Very young stands with root systems that might not fully occupy the soil were excluded. Semi-arid forests, with sparse canopy cover were also excluded from the assessment. Methods used to calculate annual root respiration included root exclusion by trenching (17 studies), elimination of root respiration by harvest or girdling (3 studies), carbon mass balance (12 studies), and modeling annual root respiration from periodic respiration measurements of excised roots (10 studies) or intact roots (2 studies).

For root exclusion methods, annual root-associated respiration was calculated as the difference between soil respiration on plots with and without roots. Root-associated respiration for these studies included CO_2 efflux produced by live roots, mycorrhizae, and microbial utilization of soil C inputs from root exudation or sloughing. Many of the studies that utilized trenching or harvest to eliminate root-associated respiration also adjusted values to account for the estimated contribution to soil respiration of CO_2 flux from decaying dead roots, or allowed time for this source of soil CO_2 efflux to subside.

Carbon mass balance methods involved subtracting measured contributors to soil respiration (e.g. decomposition of aboveground and belowground litter decomposition) from measured soil

respiration. Depending on the assumptions made, some studies estimated total ecosystem root respiration, while others estimated root-associated respiration, as defined above, or rhizosphere respiration. Rhizosphere respiration was equivalent to root-associated respiration less the contribution of mycorrhizal hyphae existing in bulk soil, away from the roots. For C mass balance methods, above- and belowground litter decomposition was either assumed to be in equilibrium with inputs or was adjusted using rates of change in soil C storage over time. Measured or published values for mycorrhizal contributions to soil respiration and rates of root C exudation were used to further adjust values in some cases, to allow estimates of the components of root-associated respiration, including the contributions of roots alone.

Studies that modeled root respiration from individual measurements first derived relationships between root respiration rate and temperature (or temperature and moisture). Data used to do this were gathered from either multiple sample dates or from manipulation of measurement conditions on a single date. These relationships were then used in conjunction with on-site measurements of root biomass and soil temperature and moisture made throughout the year, in order to estimate annual root respiration. These studies only estimate root respiration for the root size classes from which the empirical relationships were derived (indicated in Table 1).

Using the published data in Table 1, the cross-ecosystem relationship between the natural log of forest ecosystem root respiration and MAT was assessed using linear regression.

Trade-offs Between Specific Respiratory Activity and Root Biomass.

Relationships among specific root respiration rates, root biomass and MAT were assessed using published values for mid-growing season fine root respiration from 25 forests for which fine root biomass data was also available (Table 2). Fine roots in these studies were typically defined as being < 1 mm or < 2 mm in diameter. Mean annual temperature for the study locations ranged from -4.7 to 21.7 ^{o}C. Mid-growing season respiration rates were used as an indication of the greatest rate of C flow to root respiration typically occurring. Most studies (13) determined respiration rates on excised fine roots using an infra-red gas analyzers (IRGA), but IRGA measurements on intact root mats were also fairly common (9 studies). In three studies, root respiration rates were determined by dividing mid-growing season root respiration flux (g C m^{-2} s^{-1}) from trenching studies, by root biomass (g m^{-2}) for the same location.

Trade-offs between root biomass and specific root respiration rates in regulating ecosystem-level root respiration were assessed using linear regression. Fine root specific respiration rates adjusted to the median temperature of all the studies, 16 ^{o}C, were used as an indicator of fine root metabolic capacity. Published Q_{10} values for the study locations were used if available (23 studies, Table 2) to make the adjustment to 16 ^{o}C. For the two studies that did not provide a Q_{10} value, a Q_{10} of 2.5 (midway between median and mean Q_{10} values in Table 2), was used to determine a respiration rate at 16 ^{o}C. The respiration rates at 16 ^{o}C were used both to assess the relationship between metabolic capacity and root N concentration and to determine whether or not there was a tendency for metabolic capacity to decrease as MAT increased. Note that such a relationship would not preclude the possibility that realized respiration rates in the field would be higher at warmer sites, due to the effects of warmer field temperature being sufficient to counteract the lower metabolic capacity at the 16 ^{o}C reference temperature.

Root respiration Rates in Harvard Forest Soil Warming Experiments

In September, 2007, fine root (< 1 mm) respiration rates were measured in control and heated plots of three soil warming experiments at Harvard Forest. The experiments used buried heating cables to warm the soil to a target of 5 ^{o}C above ambient soil temperature (Peterjohn et al. 1994). The warming experiments varied in age and size of treated areas and included: a study with warming initiated in 1991 that utilizes 6 m x 6 m plots, with six replicates per treatment (Melillo et al. 2002); a study with warming initiated in 2003 that uses large, 30 m x 30 m, unreplicated control and heated plots; and an experiment with warming initiated in 2006, with 3 m x 3 m plots and six replicates per treatment. The ecosystems at the Harvard Forest sites are even-aged, mixed hardwood forests whose dominant tree species include paper birch, sugar and red maple, black oak and striped maple (Melillo et al. 2002).

Specific root respiration rates per gram dry weight were determined at ambient soil temperature for control (circa 15 ^{o}C on the measurement date) and heated plots (circa 21 ^{o}C on the measurement date) and at a constant reference temperature of 18 ^{o}C. Respiration rates were measured using excised roots collected with 5 cm diameter x 10 cm deep soil cores. Samples of fine roots ($\leq$ 1 mm diameter) were hand sorted from the cores and brushed free of adhering soil and organic matter, with approximately 2 g fresh weight placed in a respiration cuvette attached to an infrared gas analyzer (CIRAS-1 portable gas analyzer, PP Systems, Haverhill, MA).

Respiration was analyzed at a CO_2 concentration of 1000 $\mu l\ l^{-1}$ which approximates the concentrations typically found near the soil surface in northern hardwood forests (Burton and Pregitzer 2003). The base of the aluminum root respiration cuvette was either inserted into the soil, allowing roots inside to be maintained at ambient soil temperature during measurement, or placed in a water bath at 18 ^{o}C to enable respiration rates to be measured at the 18 ^{o}C reference temperature. Measurements at a constant reference temperature are considered to be one of the most reliable tests for the occurrence of partial acclimation in response to either seasonal changes in temperature or to warming treatments (Atkin et al. 2000). All root respiration samples were subsequently returned to the laboratory, rinsed with deionized water to remove any soil or organic matter not removed during field-cleaning prior to measurement (< 2 % of sample weight), dried for determination of actual sample weight, and analyzed for N concentration using an elemental analyzer (Carlo Erba NA 1500 NC, CE Elantech, Lakewood, NJ). One sample per plot was taken for the 1991 experiment (6 control and 6 heated). For the 2003 large plot experiment, root samples from six separate locations within each plot were measured. Samples from two control and two heated plots were measured from the 2006 experiment. Differences among experiments (1991, 2003, 2006) and warming treatments (unheated control, heated 5 ^{o}C above control) in respiration rates at ambient and reference temperatures were examined using two-factor analysis of variance. Relationships between root N and respiration rate at the 18 ^{o}C reference temperature were examined using linear regression, with differences between control and heated plots in regression slopes examined using analysis of covariance.

Soil moisture contents were measured for all experiments within four days of root respiration determination, as part of routine scheduled measurements for the experiments. Methods used included: volumetric water contents to a 5 cm depth taken 3 days after root respiration measurements for the 1991 experiment; gravimetric sampling of forest floor and surface mineral soil water contents 4 days prior to respiration measurements for the 2003 experiment; and TDR measurements taken one day after root respiration measurement for the 2006 warming experiment. Precipitation events did not occur during this week-long period.

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Table 1. Annual root respiration and fractional contribution to soil respiration for 44 forest ecosystems.

Forest Type	Location	Latitude	Longitude	MAT	MAP	Root respiration	Fraction of soil respiration	Respiration type[a]	Method	Reference
				^{o}C	mm	g C m^{-2} y^{-1}	%			
Picea mariana (Mill.) B.S.P., 150-155 y	Manitoba, Canada	55^{o}53' N	98^{o}29' W	-4.7	536	382	74	Root	Excised roots, modeled	Ryan et al. 1997
Pinus banksiana Lamb., 65-70 y	Manitoba, Canada	55^{o}56' N	98^{o}37' W	-4.7	536	314	71	Root	Excised roots, modeled	Ryan et al. 1997
Populus tremuloides Michx., 50-55 y	Manitoba, Canada	55^{o}51' N	98^{o}2' W	-4.7	536	316		Root	Excised roots, modeled	Ryan et al. 1997
Picea mariana, 115 y	Prince Albert, Canada	53^{o}59' N	105^{o}7' W	-1.5	400	143	24	Root	Carbon mass balance	Malhi et al. 1999
Picea mariana, 110-120 y	Saskatchewan, Canada	53^{o}59' N	105^{o}7' W	-1.1	405	192		Root	Excised roots, modeled	Ryan et al. 1997
Pinus banksiana, 65-70 y	Saskatchewan, Canada	53^{o}55' N	104^{o}41' W	-1.1	405	151	35	Root	Excised roots, modeled	Ryan et al. 1997, Striegl and Wickland 1998
Poplulus tremuloides, 65-70 y	Saskatchewan, Canada	53^{o}38' N	106^{o}12' W	-1.1	405	314		Root	Excised roots, modeled	Ryan et al. 1997
Picea mariana - feather moss	Saskatchewan, Canada	54^{o} N	105^{o} W	-1.1	405	124	22	Root associated	Trenching	O'Connell et al. 2003
Picea mariana - *Sphagnum*	Saskatchewan, Canada	54^{o} N	105^{o} W	-1.1	405	55	17	Root associated	Trenching	O'Connell et al. 2003
Picea mariana, 125 y	Saskatchewan, Canada	54^{o}0' N	105^{o}6' W	0.4	457	285	47	Rhizosphere	Trenching	Gaumont-Guay et al. 2008
Abies balsamea, (L.) Mill., 60 y	Eastern Canada	47^{o}19' N	71^{o}06' W	1.7		235	37	Root associated	Trenching[b]	Lavigne et al. 2003
Abies balsamea, 50 y	Eastern Canada	47^{o}44' N	68^{o}09' W	3.1		660	57	Root associated	Trenching[b]	Lavigne et al. 2003
Pinus sylvestris L. 45-55 y	Sweden	64^{o}14' N	19^{o}45' E	3.8	670	837	47	Root associated	Girdling	Majdi et al. 2007, Hogberg et al. 2002
Mixed *Fagus grandifolia* Ehrh., *Acer saccharum* Marsh., *Betula alleghaniensis* Britt., 90 yr	Hubbard Brook New Hampshire, USA	43^{o}56' N	71^{o}45' W	4.5	1400	260	39	Root	Excised roots, modeled	Fahey et al. 2005

Pinus resinosa Ait. plantation, 31 y	Wisconsin, USA	46°10' N	89°40' W	4.6	586[c]	362	42	Root associated	Trenching	Haynes and Gower 1995
Mixed *Quercus rubra* L., *Acer rubrum* L., *Betula papyrifera* Marsh., 80 y	Harvard Forest USA	42°30' N	72°12' W	6.0	1100	123	33	Root	Trenching	Bowden et al. 1993
Quercus crispula Blume, *Betula ermanii* Cham., 40 y	Central Honshu, Japan	36°8' N	137°26' E	6.1	2175	380	45	Root associated	Trenching	Lee et al. 2005a
Abies balsamea, 40 y	Eastern Canada	46°02' N	66°23' W	6.2		980	65	Root associated	Trenching[b]	Lavigne et al. 2003
Fagus crenata Blume, *Abies homolepis* Sieb. et Zucc., old growth	Nara prefecture, Japan	34° N	135° E	7.0[e]		210	42	Root	Carbon mass balance	Nakane 1980
Alnus glutinosa (L.) Gaertn.,45 y	Kiel Ecosystem Research Center, Germany	54°6' N	10°14' E	8.1	697	1234	70	Rhizosphere	Intact roots, modeled	Kutsch et al. 2001, Dilly et al. 2000
Pseudotsuga menziesii (Mirb.) Franco, 56 y	Coastal British Columbia, Canada	49°15' N	125°19' W	8.6	1452	420	35	Rhizosphere	Cylinders with root exclusion mesh	Lalonde and Prescott 2007
Old-growth *Pseudotsuga menziesii*, *Tsuga heterophylla* (Raf.) Sarg.	Oregon cascades, USA	44°15' N	122°10' W	8.7	2370	185	23	Rhizosphere	Trenching	Sulzman et al. 2005
Fagus sylvatica L. 30 y	France	48°40' N	7°5' E	9.2	820	396	60	Root associated	Trenching	Epron et al. 1999
Old-growth *Nothofagus fusca* (Hook. f.) Oerst.	South Island, New Zealand	42°13' S	172°15' E	9.8	1520	160	23	Root	Excised roots, modeled	Tate et al. 1993
Quercus serrata Thunb., 102 yr	Hiroshima prefecture, Japan	34°11'	132°8' E	12.1	2174	484	51	Root associated	Pre- and post-harvest[b]	Nakane et al. 1996
Pinus ponderosa Dougl. ex. Laws., 14 y	California, USA	38°54' N	120°38' W	12.5	1290	524	44	Root associated	Trenching	Tang et al. 2005
Pinus ponderosa plantation, 13 y	California, USA	38°54' N	120°38' W	13.0	1290	524	44	Root associated	Trenching	Tang et al. 2005
Quercus sessilifolia Blume, *Castanopsis cuspidata* (Thunb.) Schottky, old growth	Nara prefecture, Japan	35° N	135° E	13.1[e]		570	51	Root	Carbon mass balance	Nakane 1980
Liriodendron tulipifera L., 50 y	Oak Ridge, Tennessee, USA	35°57' N	84°17' W	13.3	1265	372	35	Root	Excised roots, modeled	Edwards and Sollins 1973; Edwards and Harris 1977
Pinus radiata D. Don, 20 y	Canberra, Austrailia	35°21' S	148°56' E	13.5	791	769[d]	78	Root	Intact roots, modeled	Ryan et al. 1996

Quercus cerris L., 1 y coppice	Italy	43°24' N	11°55' E	14.0	755	210	23	Root associated	Trenching	Rey et al. 2002
Quercus, *Carya*	Oak Ridge, Tennessee, USA	35°57' N	84°17' W	14.0	1400	395	53	Root	Carbon mass balance	Malhi et al. 1999
Pinus densiflora Sieb. et Zucc., 80 yr	Hiroshima City, Japan	34° N	134 °E	15.0	1544	603	47	Root associated	Pre- and post-harvest[b]	Nakane et al. 1983
Pinus taeda L., 16 y	North Carolina, USA	35°97' N	79°09' W	15.8	1145	394		Fine root (< 1 mm)	Excised roots, modeled	Matamala and Schlesinger 2000
Pinus elliotti Engelm. plantation 29 yr	Florida, USA	29°44' N	82°9' W	21.7	1342	810	62	Root associated	Trenching	Ewel et al. 1987b
Pinus elliotti plantation 9 yr	Florida, USA	29°44' N	82°9' W	21.7	1342	430	51	Root associated	Trenching	Ewel et al. 1987b
Tropical rain forest, old growth	West Malaysia	3° N	102° E	25.1[e]		700	49	Root	Carbon mass balance	Nakane 1980
Tropical forest	Manaus, Brazil	2°35' S	50°06' W	25.5	2200	680	41	Root	Carbon mass balance	Malhi et al. 1999
Hyeronima alchorneoides Allemão plantation, 16 y	La Selva, Cosa Rica	10°26' N	83°59' W	25.8	3900	820	40	Rhizosphere	Carbon mass balance	Valverde-Barrantes 2007
Pentaclethra macroloba (Willd) Kuntze plantation, 16 y	La Selva, Cosa Rica	10°26' N	83°59' W	25.8	3900	890	50	Rhizosphere	Carbon mass balance	Valverde-Barrantes 2007
Pinus patula ssp. *tecunumanii* (Eguiluz & J.P. Perry) Styles plantation, 16 y	La Selva, Cosa Rica	10°26' N	83°59' W	25.8	3900	890	55	Rhizosphere	Carbon mass balance	Valverde-Barrantes 2007
Virola koschyna Warb. plantation, 16 y	La Selva, Cosa Rica	10°26' N	83°59' W	25.8	3900	1100	62	Rhizosphere	Carbon mass balance	Valverde-Barrantes 2007
Vochysia guatemalensis Donn. Sm. plantation, 16 y	La Selva, Cosa Rica	10°26' N	83°59' W	25.8	3900	1340	57	Rhizosphere	Carbon mass balance	Valverde-Barrantes 2007
Tropical forest	Brazilian state of Pará	2°59' S	47°31' W	25.8	1750	1510	63	Root	Carbon mass balance	Trumbore et al. 1995

[a]Root respiration includes only roots; root associated respiration includes root respiration, mycorrhizal respiration and microbial respiration of root exudates; and rhizosphere respiration is the equal to root associated respiration less the respiration of mycorrhizal hyphae extending into the bulk soil.
[b]Soil respiration rates in trenched or harvested plots were adjusted for dead root decomposition when calculating root-associated respiration by difference from control plot root respiration.

[c]Precipiation is for growing season only.

[d]Value for root respiration would be 274 if adjustment recommended by Ryan et al. (1996) for measuring root respiration at atmospheric [CO2] is included.

[e]Data are for mean annual soil temperature.

Table 2. Mid-growing season fine root respiration and fine root biomass for 25 forest ecosystems.

Forest Type	Location	Lati-tude	Longi-tude	MAT	MAP	Root respi-ration	Measure-ment temperature	Time of year	Fine root N	Fine root mass	Q_{10}	Root dia-meter	Method	Reference
				^{o}C	mm	nmol g^{-1} s^{-1}	^{o}C		g kg^{-1}	g m^{-2}		mm		
Picea mariana, 150-155 y	Manitoba, Canada	55°53' N	98°29' W	-4.7	536	7.2	10.0	June-August		170	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Pinus banksiana, 65-70 y	Manitoba, Canada	55°56' N	98°37' W	-4.7	536	7.1	10.0	June-July		205	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Populus tremuloides, 50-55 y	Manitoba, Canada	55°51' N	98°2' W	-4.7	536	3.9	10.0	June-July		158	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Populus balsamifera, L., 80-100 y	Alaska, USA	64°40' N	148o15' W	-3.3	287	3.0	8.4	Mid-June	14.9	472	2.4	< 1	Excised roots	Burton et al. 2002, Ruess et al. 1996
Picea glauca (Moench) Voss, 200-300 y	Alaska, USA	64°41' N	148o14' W	-3.3	287	2.9	10.8	Mid-June	10.6	288	2.9	< 1	Excised roots	Burton et al. 2002, Ruess et al. 1996
Picea mariana, 160-200 y	Alaska, USA	64°48' N	147o52' W	-3.3	269	1.8	8.0	Mid-June	9.1	1776	2.3	< 1	Excised roots	Ruess et al. 2003, Burton unpublished
Picea mariana, 110-120 y	Saskatchewan, Canada	53°59' N	105o7' W	-1.1	405	4.4	10.0	June-July		77	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Pinus banksiana, 65-70 y	Saskatchewan, Canada	53°55' N	104°41' W	-1.1	405	3.9	10.0	June-July		90	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Poplulus tremuloides, 65-70 y	Saskatchewan, Canada	53°38' N	106°12' W	-1.1	405	6.2	10.0	June-July		79	1.9	< 2	Intact root mats	Ryan et al. 1997, Steele et al. 1997
Picea mariana, 80 y	Saskatchewan, Canada	53°50' N	105°30'	1.5	389	10.2	15.0	July		398		< 1	Excised roots	Uchida et al. 1998
Larix gmelini (Rupr.) Rupr., 17 y	Northeast China	45°20' N	127°34' E	2.8	724	6.6	17.0	August	14.8	606	5.6	all	Trenched plots	Jiang et al. 2005
Larix gmelini (Rupr.) Rupr., 31 y	Northeast China	45°20' N	127°34' E	2.8	724	5.0	17.0	August	14.4	357	4.2	all	Trenched plots	Jiang et al. 2005

Acer saccharum, 94 y	Michigan, USA	46°52' N	88°53' W	4.8	821	7.4	17.5	June-August	18.5	571	2.7	< 1	Excised roots	Burton et al. 2004
Pinus sylvestris, *Picea abies*, 34-105 y	Uppsala, Sweden[a]	60°5' N	17°30' W	5.5	527	2.3	14.0	July-August	6.5	613	5.0	< 5[b]	Intact root mats	Widen and Majdi 2001
Acer saccharum, 88 y	Michigan, USA	45°33' N	84°51' W	6.1	828	9.8	20.0	June-August	19.6	439	2.7	< 1	Excised roots	Burton et al. 2004
Quercus crispula, *Betula ermanii*, 40 y	Central Japan	36°80' N	137°26' E	6.1	2175	3.7	16.0	July		673		all	Trenched plots	Lee et al. 2003
Acer saccharum, 89 y	Michigan, USA	44°23' N	85°50' W	6.9	856	6.9	19.1	June-August	19.4	392	2.7	< 1	Excised roots	Burton et al. 2004
Acer saccharum, 93 y	Michigan, USA	43°40' N	86°09' W	7.6	793	5.6	19.4	June-August	18.7	485	2.7	< 1	Excised roots	Burton et al. 2004
Betula, Quercus, Tilia	North Carolina, USA	35°3' N	83°25' W	9.4	2607	4.7	18.2	Early June	15.0	620	2.4	< 1[c]	Excised roots	Burton et al. 2002, Davis et al. 2004
Quercus, Carya	North Carolina, USA	35°3' N	83°25' W	11.1	2502	4.2	17.8	Early June	12.9	740	3.1	< 1[c]	Excised roots	Burton et al. 2002, Davis et al. 2004
Lirodendron tulipifera, 40 y	North Carolina, USA	35°4' N	83°26' W	12.7	1816	10.6	19.3	Early June	20.7	468	2.6	< 1[c]	Excised roots	Burton et al. 2002, Davis et al. 2004
Pinus radiata, 20 y	Canberra, Australia	35°25' S	148°56' E	13.5	791	10.4[d]	21.0	January	7.4	257	2.0	< 2	Intact root mats	Ryan et al. 1996
Pinus elliottii plantation, 17 y	Florida, USA	30°37' N	81°43' W	20.0	1303	6.3	26.5	Early June	9.6	205	2.5	< 1[c]	Excised roots	Burton et al. 2002, Shan et al. 2001
Pinus elliottii plantation, 24 y	Florida, USA	29°44' N	82°9' W	21.7	1342	4.5	28.0	Summer		870	2.1	< 2	Intact roots	Gholz et al. 1991, Cropper and Gholz 1991, Ewel et al. 1987a
Eucalyptus urophylla x *Eucalyptus grandis*, 3 y	Congo-Brazzaville, central Africa	4° S	12° E	25.0	1400	10.3	30.0	April-June		193	2.2	< 2	Excised roots	Marsden et al. 2008

[a]Average of sites with 3 aspects, SW, N and S.

[b]90% of roots < 2 mm.

[c]Biomass value is for all roots < 2 mm.

[d]Published respiration for 15 °C was adjusted upward using a Q_{10} of 2. Adjustment for measuring respiration at atmospheric [CO_2] rather than soil [CO_2] was not performed.

Table 3. Surface soil moisture contents for three Harvard Forest soil warming experiments in September, 2007.

Experiment	Moisture units	Control	Heated	*P* value
1991	volumetric %	6.4 (0.2)	5.7 (0.4)	0.153
2003 – forest floor	gravimetric %	50.3 (6.8)	35.2 (2.4)	0.044
2003 – surface soil	gravimetric %	27.8 (1.2)	22.9 (0.7)	0.002
2006	TDR (volumetric %)	11.6 (0.8)	9.7 (0.3)	0.051

Values are the mean, with standard error in parentheses. TDR = time-domain reflectometry.

Figure Legends.

Figure 1. Increase in forest ecosystem annual root respiration (g C m^{-2} of ground area) with increasing mean annual temperature (MAT). The solid line is for all data: ln(respiration) = 5.501 + 0.049 x MAT (r^2 = 0.43; P < 0.001). The dashed line is for boreal and temperate data, excluding four data points identified as outliers (i.e. the boreal and temperate points located well above the line): ln(respiration) = 5.383 + 0.045 x MAT (r^2 = 0.33; P < 0.001).

Figure 2. Relationships between MAT and specific root respiration rates measured during the warm portion of the growing season (A; r = 0.40, *P* = 0.05) and root metabolic capacity (B; r = -0.51, *P* = 0.01). Mid-growing season specific root respiration rates adjusted to a common reference temperature of 16 ^{o}C were used as an index of root metabolic capacity.

Figure 3. Decrease in root biomass with increasing specific respiration rates at mid-growing season (A) and with increasing root metabolic capacity (B). Mid-growing season specific root respiration rates adjusted to a common reference temperature of 16 ^{o}C were used as an index of root metabolic capacity. The trendline in (A) is for non-boreal forests only (r = -0.63, P = 0.02). The trendline in (B) is for all data (r = -0.46, *P* = 0.02), except an outlier with extremely high biomass of 1776 g m^{-2} and low respiration (data point not shown, but see Table 2).

Figure 4. Specific root respiration rates at ambient soil temperature (A), specific respiration rates at a reference temperature of 18 ^{o}C (B), and N concentration (C) for fine roots (< 1 mm) from control and heated plots for three Harvard Forest soil warming studies. Ambient soil temperatures for the control and heated treatments on the measurement date are indicated on the data bars in (A). Soil warming significantly increased respiration rate at ambient treatment temperature (*P* = 0.009) and significantly decreased respiration rates measured at the 18 ^{o}C reference temperature (*P* = 0.003). Horizontal lines in (A) indicate expected respiration rates for the warmed plots if rates observed for the control plots were exponentially increased from control plot temperature to heated plot temperature using the average Q_{10} for root respiration of 2.7 from the studies listed in Table 2.

Figure 5. Relationships between fine root respiration and fine root N concentration for all data from the three Harvard Forest soil warming experiments. The linear relationship for the warmed plots (dashed line) has a similar slope, but significantly lower intercept ($P < 0.001$), than that for the control treatment (solid line).

Figure 6. Linear increase in specific respiration rate at 16 ^{o}C with N concentration ($r = 0.59$, $P = 0.02$) for the studies listed in Table 2.

Figure 1.

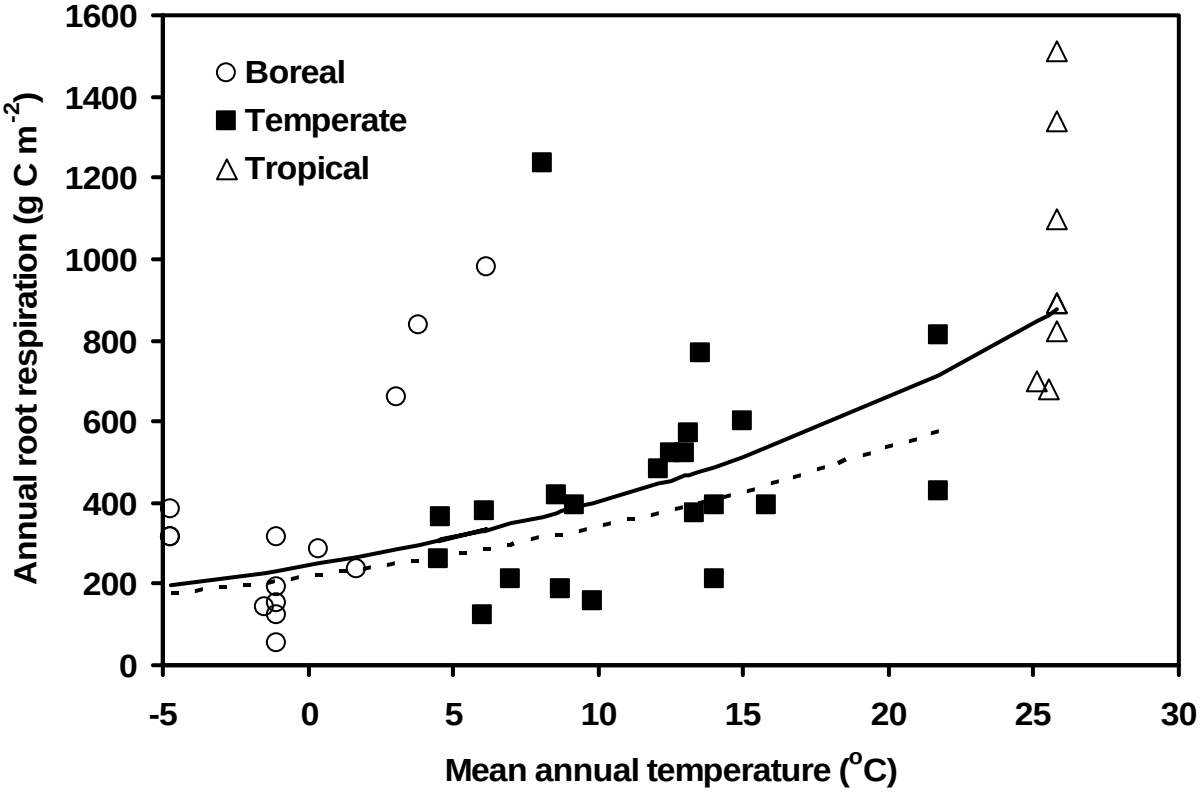
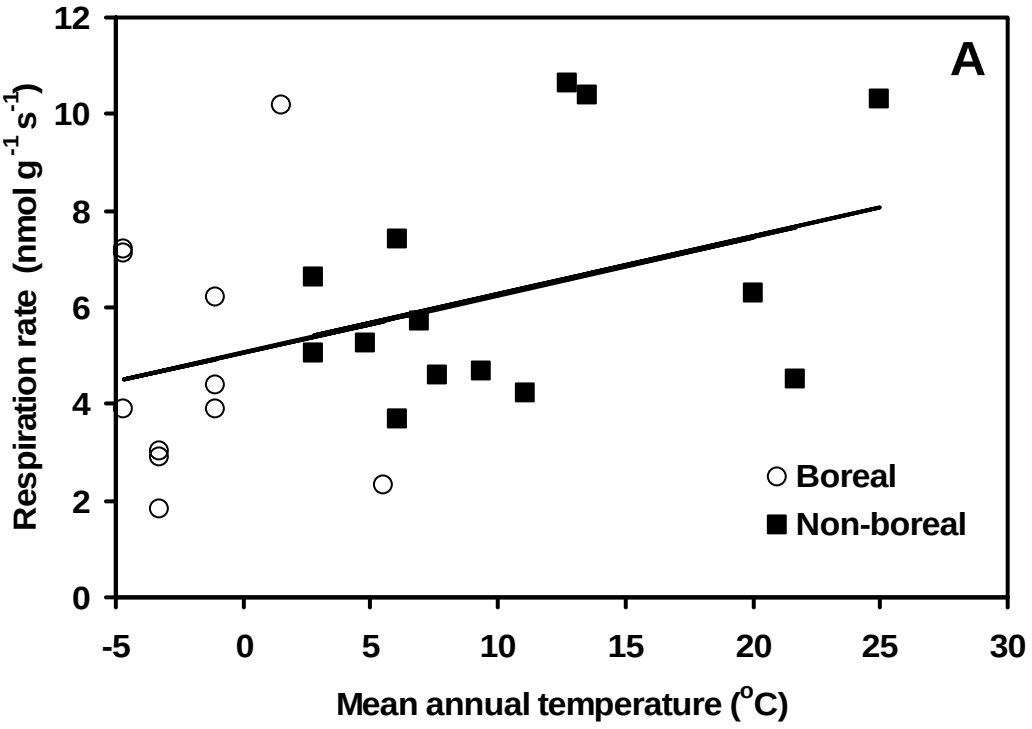

Boreal
Temperate
Tropical
Annual root respiration (g C m-2)
Mean annual temperature (°C)
0
200
400
600
800
1000
1200
1400
1600
-5
0
5
10
15
20
25
30

Figure 2.


A
Respiration rate (nmol g-1 s-1)
Mean annual temperature (°C)
Boreal
Non-boreal
0
2
4
6
8
10
12
-5
0
5
10
15
20
25
30

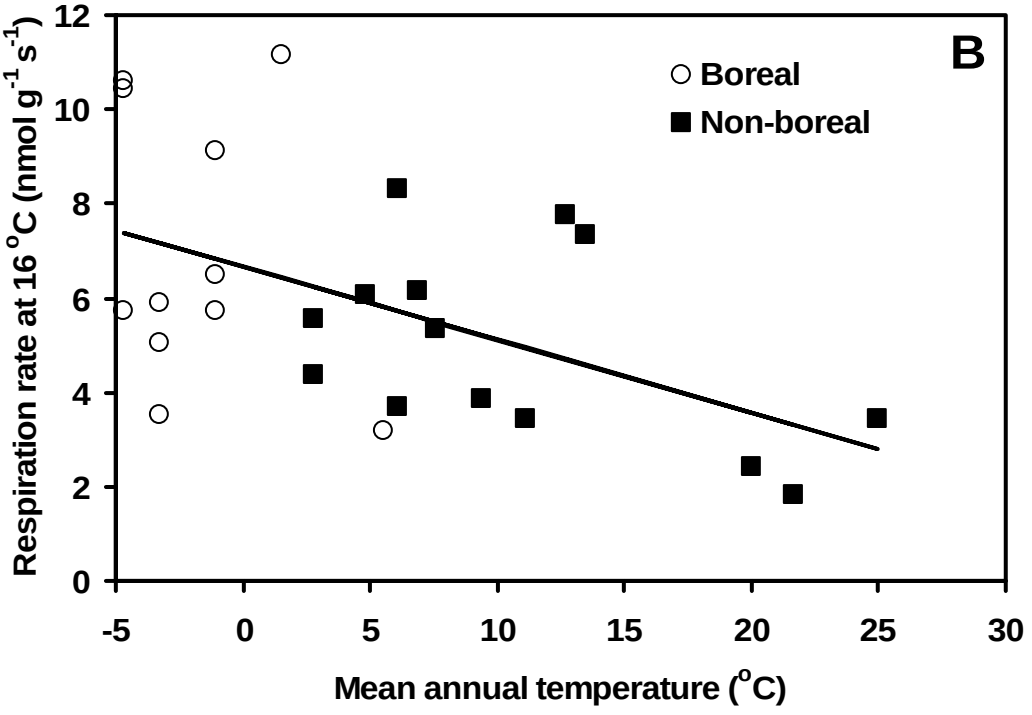
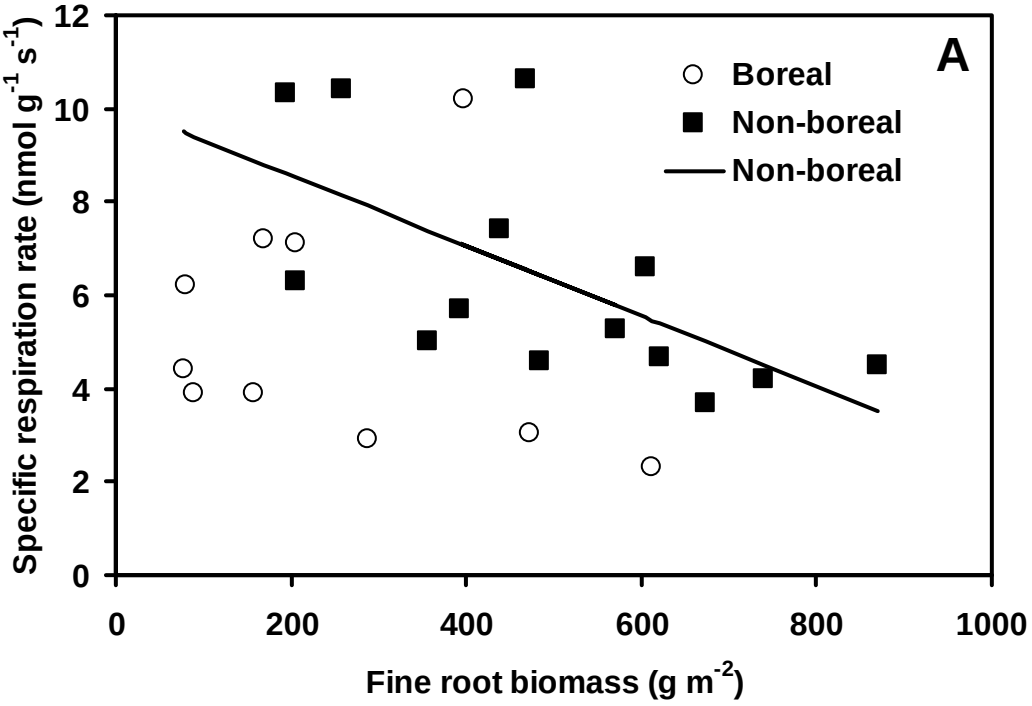

B
Respiration rate at 16 °C (nmol g-1 s-1)
Mean annual temperature (°C)
Boreal
Non-boreal
0
2
4
6
8
10
12
-5
0
5
10
15
20
25
30

Figure 3.


A
Boreal
Non-boreal
Non-boreal
Specific respiration rate (nmol g-1 s-1)
Fine root biomass (g m-2)
0
2
4
6
8
10
12
0
200
400
600
800
1000

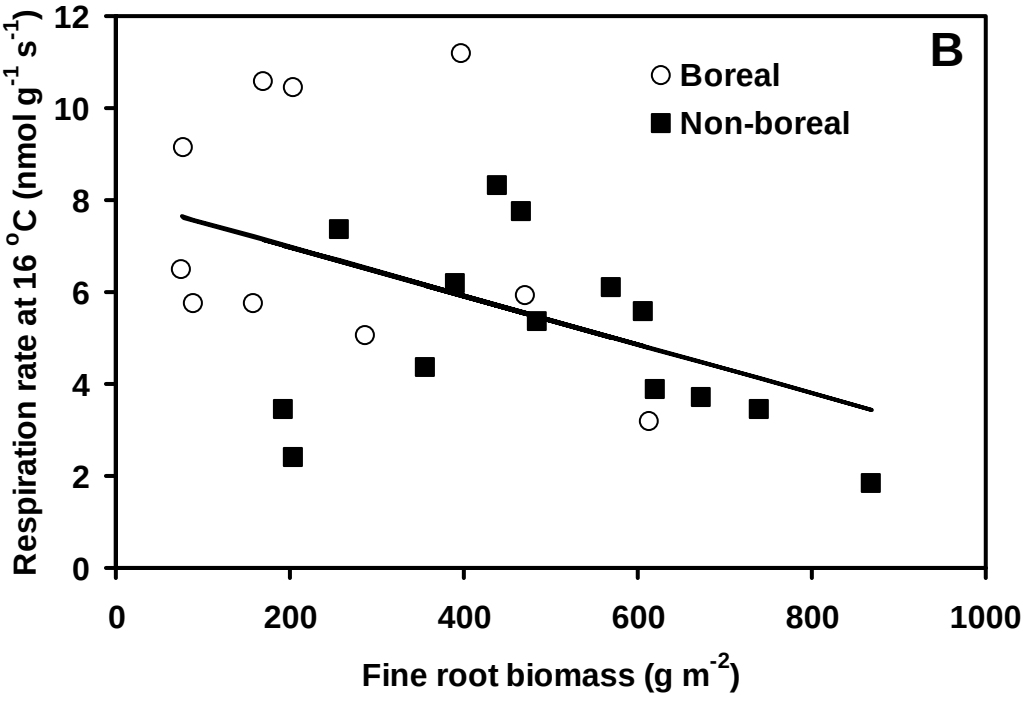

B
Boreal
Non-boreal
Respiration rate at 16 °C (nmol g-1 s-1)
Fine root biomass (g m-2)
0
2
4
6
8
10
12
0
200
400
600
800
1000

Figure 4.

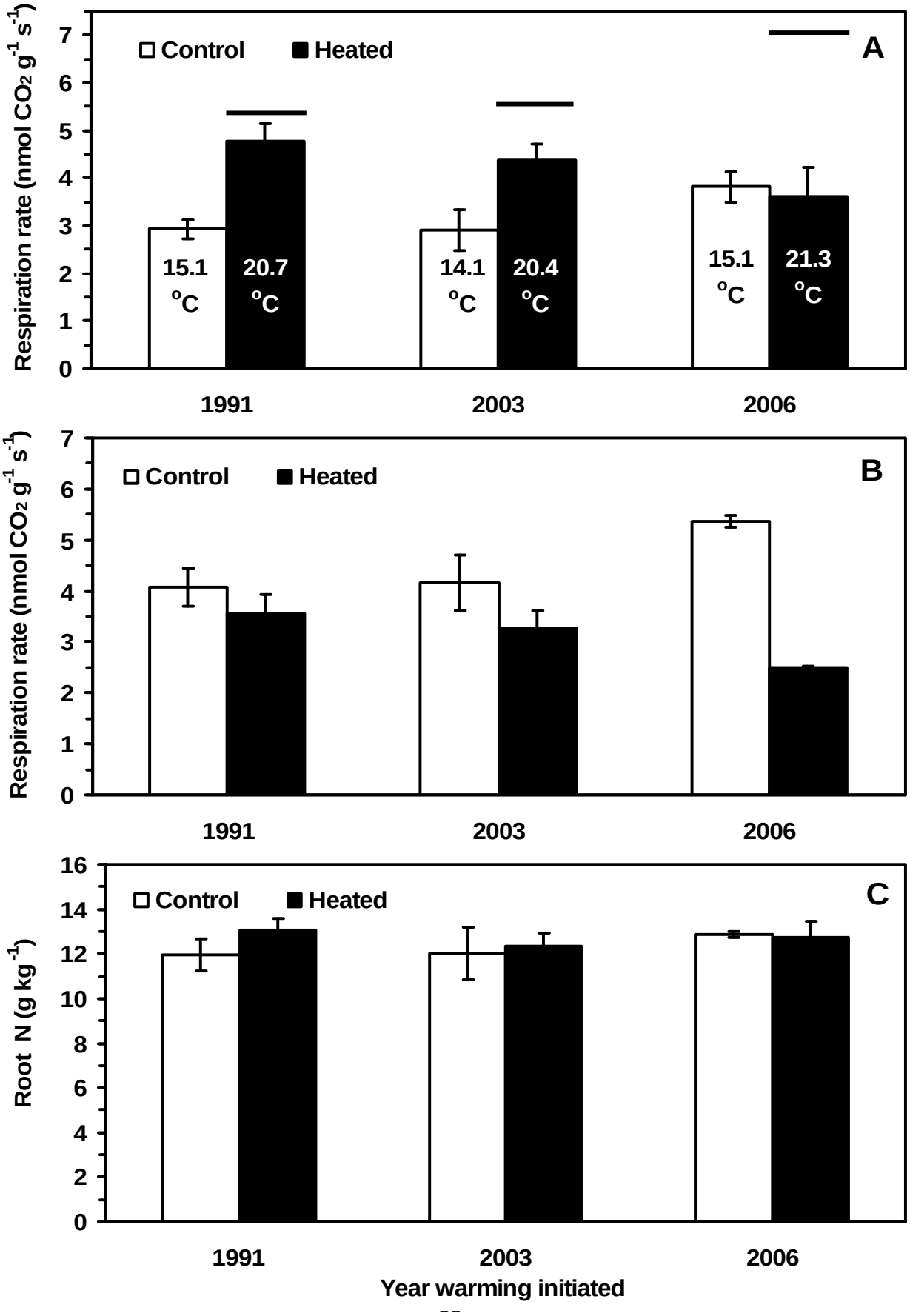

A
Control
Heated
Respiration rate (nmol CO2 g-1 s-1)
0
1
2
3
4
5
6
7
15.1 °C
20.7 °C
14.1 °C
20.4 °C
15.1 °C
21.3 °C
1991
2003
2006
B
Control
Heated
Respiration rate (nmol CO2 g-1 s-1)
0
1
2
3
4
5
6
7
1991
2003
2006
C
Control
Heated
Root N (g kg-1)
0
2
4
6
8
10
12
14
16
1991
2003
2006
Year warming initiated

Figure 5.

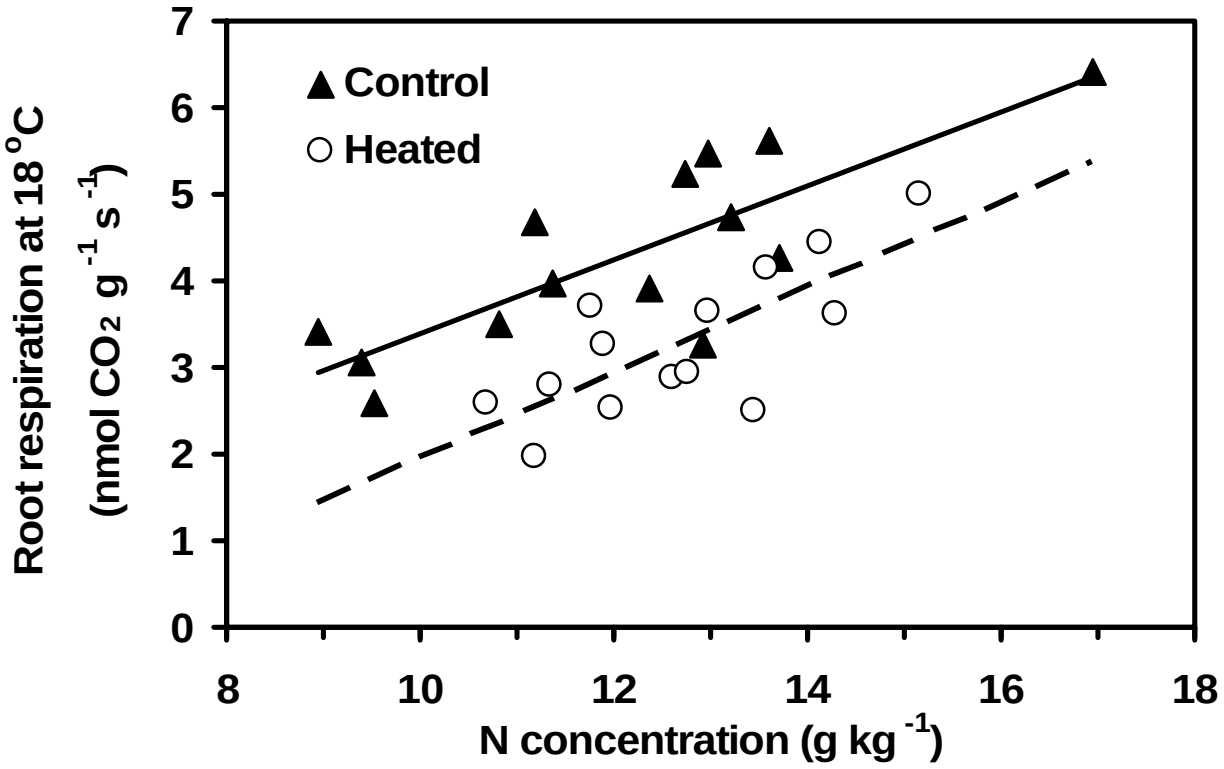
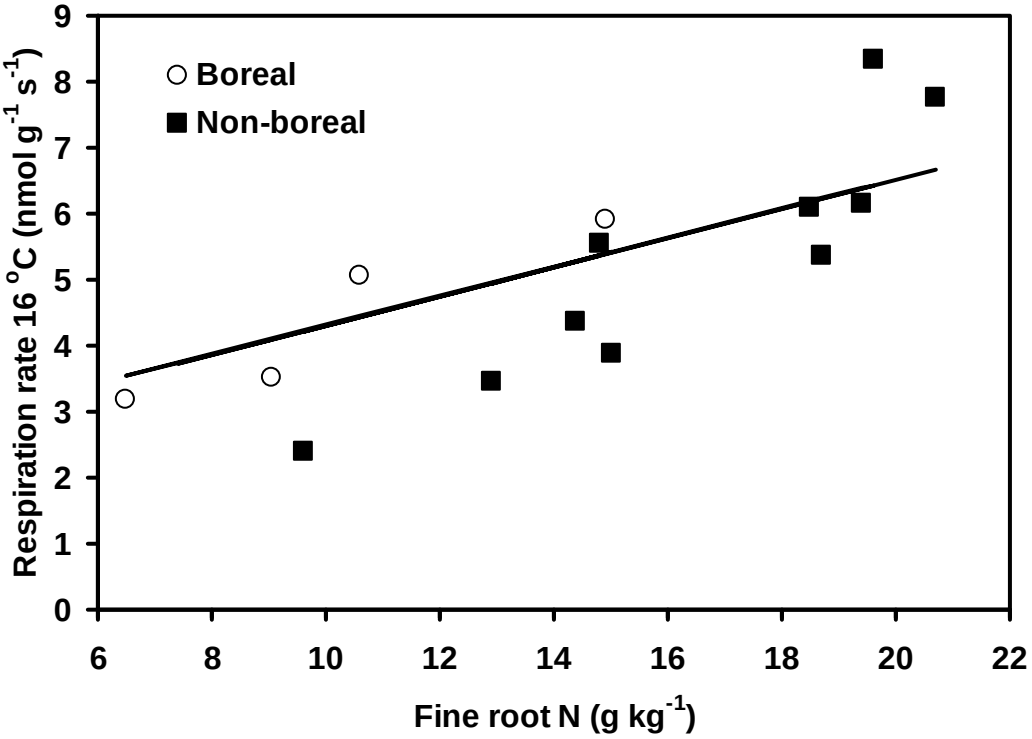

Control
Heated
Root respiration at 18 °C
(nmol CO2 g-1 s-1)
N concentration (g kg-1)
0
1
2
3
4
5
6
7
8
10
12
14
16
18

Figure 6.


Boreal
Non-boreal
Respiration rate 16 °C (nmol g-1 s-1)
Fine root N (g kg-1)
0
1
2
3
4
5
6
7
8
9
6
8
10
12
14
16
18
20
22